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Invited review

When tree rings go global: Challenges and opportunities for retro- and prospective insight

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ABSTRACT

The demand for large-scale and long-term information on tree growth is increasing rapidly as environmental change research strives to quantify and forecast the impacts of continued warming on forest ecosystems. This demand, combined with the now quasi-global availability of tree-ring observations, has inspired researchers to compile large tree-ring networks to address continental or even global-scale research questions. However, these emergent spatial objectives contrast with paleo-oriented research ideas that have guided the development of many existing records. A series of challenges related to how, where, and when samples have been collected is complicating the transition of tree rings from a local to a global resource on the question of tree growth. Herein, we review possibilities to scale tree-ring data (A) from the sample to the whole tree, (B) from the tree to the site, and (C) from the site to larger spatial domains. Representative tree-ring sampling supported by creative statistical approaches is thereby key to robustly capture the heterogeneity of climate-growth responses across forested landscapes. We highlight the benefits of combining the temporal information embedded in tree rings with the spatial information offered by forest inventories and earth observations to quantify tree growth and its drivers. In addition, we show how the continued development of mechanistic tree-ring models can help address some of the non-linearities and feedbacks that complicate making inference from tree-ring data. By

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embracing scaling issues, the discipline of dendrochronology will greatly increase its contributions to assessing climate impacts on forests and support the development of adaptation strategies.

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1. Introduction

1.1. An increasing need to scale tree-ring data

Climate change during the Anthropocene is now considered a certainty (Marotzke et al., 2017) and environmental research focuses increasingly on quantifying and forecasting the impacts of continued warming on ecosystems and natural resources. Forests receive particular attention because they absorb large amounts of excess atmospheric CO_2 generated by human activities (Le Quéré et al., 2016) and store this carbon in woody biomass for decades to centuries (Körner, 2017). Importantly, rising temperatures can have either beneficial or detrimental effects on forests, depending on their present climatic limitations (Babst et al., 2013; Charney et al., 2016; St George and Ault, 2014). For instance, climate warming in cold-humid areas can stimulate tree growth through a prolonged growing season and more rapid cellular development (Cuny et al., 2014; Rossi et al., 2016). In drier regions, a warming-induced increase in atmospheric water demand triggers physiological responses in trees that lower hydraulic conductivity, reduce the production and allocation of carbohydrates to structural growth, and ultimately increase tree mortality (Adams et al., 2017). This continuum of possible consequences from warming provides an incentive to understand how changes in the biotic and abiotic environment affect forest ecosystem processes across a range of spatial and temporal scales.

Measurements of secondary growth patterns in trees, shrubs, and perennial herbs (subsequently called “tree rings”) are the primary resource to retrospectively provide tree growth information across large environmental gradients and at sub-annual to multi-centennial time scales. Such data are increasingly used to study the impacts of global change on forest ecosystems. A number of recent studies have compiled large tree-ring networks to hind- and forecast forest growth variability in response to climate (Babst et al., 2013; Charney et al., 2016; Martin-Benito and Pederson, 2015; Restaino et al., 2016; St George and Ault, 2014; Tei et al., 2017), track the recovery of growth after extreme events (Anderegg et al., 2015; Wu et al., 2017), relate growth variability to canopy dynamics (Vicente-Serrano et al., 2016; Seftigen et al., in press), or search for signals of CO_2 fertilization (Frank et al., 2015; Gedalof and Berg, 2010; Girardin et al., 2016; Peñuelas et al., 2011). In addition, tree-ring data are increasingly used to quantify aboveground biomass increment (Babst et al., 2014b), improve our physiological understanding of wood formation (Rathgeber et al., 2016), and calibrate mechanistic models for climate reconstruction (Guiot et al., 2014).

Tree-ring records are available on all forested continents (Babst et al., 2017; Brienen et al., 2016), inviting the use of existing and the development of new tree-ring archives for a variety of research contexts. However, tree rings remain a very local and variable product of tree-internal processes that are modulated by a tree's immediate biotic and abiotic environment (Rathgeber et al., 2016). Inference and prediction at large spatial scales based on such local data (involving scaling, interpolation, and projection; Table 1) is challenging and introduces uncertainty that researchers need to be aware of and – to the extent possible – quantify (Fig. 1). Scaling is complicated by heterogeneity (Scholes, 2017), for example when a tree-ring collection insufficiently represents forest structure, composition, and disturbance regimes across a landscape. Dendrochronologists often counteract heterogeneity by increasing the number of collected samples per tree, site, or region. This approach can indeed reduce uncertainties around the mean record for the desired scale (e.g. a site or regional chronology), but its success for improving spatial representation of tree growth critically depends on the underlying sampling strategy (see below). Another challenge for scaling is that fixed statistical relationships derived from a given dataset may not capture the high dimensionality in driver and response variables, their couplings, non-linear processes and feedbacks. This calls for a better understanding of the true variability in the system and ideally for mechanistic process representation to model tree growth (see Section 4). Given the above context, we find it prudent to briefly pause and examine the potential and challenges associated with scaling tree-ring information before making large-scale inference. Herein, we address the following three upscaling steps:

(A) **From the sample to the whole tree**: Tree-ring samples are collected as cross-sections, increment cores, or micro-cores. Regardless of the shape or size of samples, individual measurements capture growth only at one position along/around the stem, branch, or root. Multiple samples are thus often collected from the same individual to better capture its growth variability. After visually and statistically ensuring correct dating of each annual growth ring (i.e. “crossdating”; Black et al., 2016; Stokes and Smiley, 1968), the measurements of all samples are generally combined to represent the radial growth of the individual. This first step of upscaling (Table 1) usually involves averaging or pooling, but the representation of tree-level change may be with raw measurements, detrended and/or standardized tree-ring indices, conversion to basal area increment, or other forms of allometric scaling or structural modeling.

(B) **From the tree to the site**: A “site” is the area that encompasses the sampled individuals. Upscaling to the site level means combining the measurements from all individuals into one or multiple time series that are usually referred to as “chronologies”. An underlying assumption is thereby that the site is a subsample of a population of trees and the derived chronology is typically regarded as the best estimate of this population's growth variability (Wigley et al., 1984). The criteria for sampling trees within a site vary according to the aims of a given study. For example, old and dominant individuals are selectively sampled for dendroclimatic reconstructions; plot designs, stratified or random samplings are often preferred for dendroecological studies; and trees with specific characteristics (e.g. scars) are targeted to assess the natural disturbance history of a site. Researchers are also interested in within-site variability that is driven by micro-site conditions (e.g. topography Salzer et al., 2014) and may contain relevant ecological information that is otherwise averaged out when only a mean site chronology is calculated (Buras et al., 2016; Peters et al., 1981).

(C) **From the site to larger spatial scales**: Site records are compiled into tree-ring networks to cover regions or

Table 1
Definitions of important terms used in this review (partly inspired by Scholes, 2017).

Term	Definition
Scale *(noun)*	Spatial extent and/or temporal duration.
Scale *(verb)*	Extrapolation or projection of a result from one scale to another. Herein, we focus primarily on the scaling of forest growth and biomass increment (as opposed to, e.g., scaling from local to global temperature variations; Neukom et al., 2014). Linear scaling (i.e., proportional or additive scaling) assumes that the driving processes are homogeneous over the scale range and that no interactions in space or time impose non-linearities. An example is the scaling of forest biomass increment from a sample of 0.1-ha forest plots to a 10,000-ha landscape. If heterogeneities (e.g., in forest type or time-since-disturbance) make simple linear scaling inaccurate, power-law scaling can capture nonlinearities across scales. For example, the scaling of bole diameter to whole-tree biomass involves allometric (power-law) equations, that are usually empirically derived, but may be (quasi-)mechanistic.
Downscaling	The process of disaggregation of a result to a smaller scale; i.e., a few-to-many problem. Climate system downscaling is a well-known example. The aggregated result is known; the challenge is to assign values (along with uncertainty) to the underlying subunits, according to some information about their heterogeneity.
Upscaling	The process of aggregation to a larger scale; i.e., a many-to-few problem. An example is the upscaling of information from many trees within a site to a single site-level estimate (e.g. a mean site chronology). Another example is the summing of biomass increment estimates from all trees in a forest plot to reach a stand-level estimate of biomass increment.
Resolution	Also known as "grain", the smallest measurement unit in either space or time.

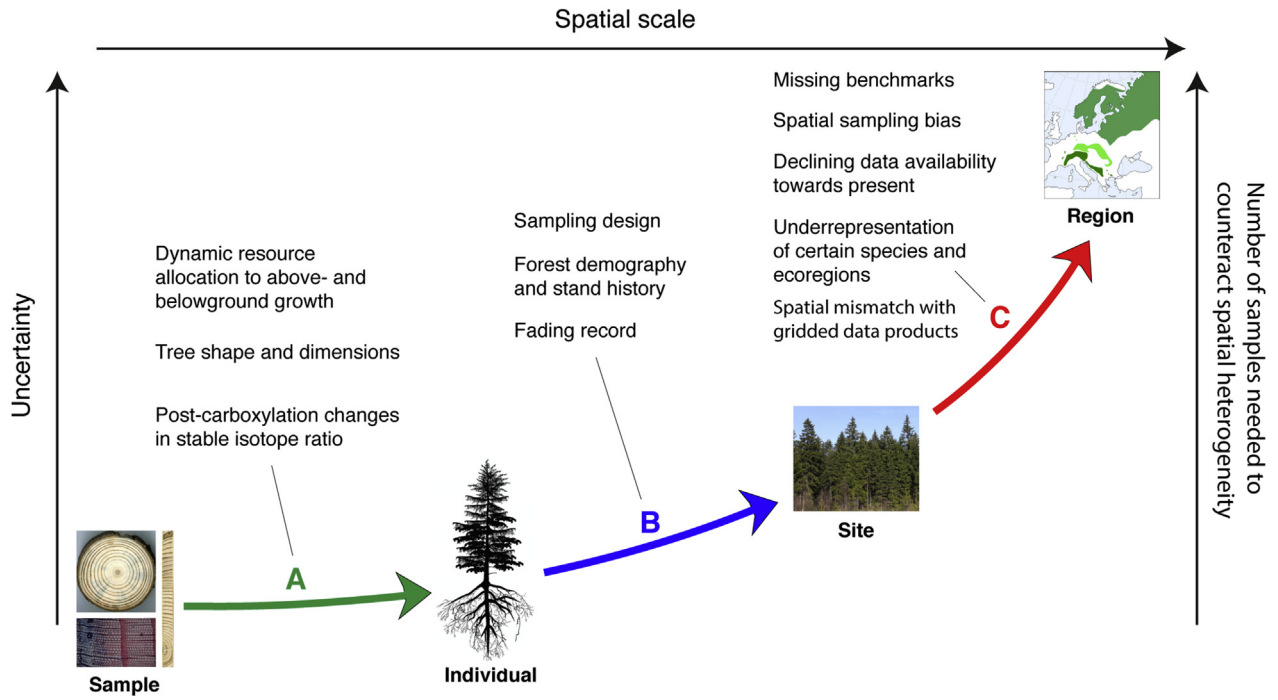

Fig. 1. Overview of the different spatial scales and propagating uncertainty associated with the scaling of tree-ring data. Sources of uncertainty are listed for each scaling step (A–C) using Norway spruce (*Picea abies*) as an example. The sample images are adapted from (Babst et al., 2014a) and the species distribution map is from lutherie.net/eurospruce. If scaling steps A-C are carefully followed and uncertainties are adequately considered, tree-ring data can theoretically meet the demand for global information on long-term forest growth. In practice, however, a series of challenges related to how, where, and when samples have been collected accompanies the transition of tree rings from a local to a global data resource (see Section 1.2).

continents. Depending on the research question, these networks are either assessed in their entirety, or sites may be grouped and analyzed by species (Zhang et al., 2018), growth variability (Seim et al., 2015), growth trends (Hellmann et al., 2016), climate response (Babst et al., 2013; Björklund et al., 2017; Charney et al., 2016; Martin-Benito and Pederson, 2015), or biogeography (Girardin et al., 2016). Moreover, spatial assessments often include analyses of climate-growth relationships – sometimes combined with clustering techniques, dimension reduction, or embedded in a machine learning framework (see Section 2.2.1). The resulting regional records are assumed to represent the geographic space covered by the underlying tree-ring network, an assumption that will need thorough testing in the future (see Sections 2 and 5).

1.2. Challenges associated with scaling tree-ring data

Environmental systems are best represented if the collected data are extensive and distributed systematically or randomly across the target space (e.g. geographic or bioclimatic space). This is not the case for the vast majority of existing tree-ring records, in part because scaling was historically not the goal of dendrochronological sampling. Instead, data collection strategies and methods have been driven by study-specific goals, for example to date archaeological material, detect disturbance events, reconstruct climate, or assess the co-variation of tree growth with an environmental variable. Moreover, the scope of tree-ring research has continuously been expanded to include ecophysiology (Levesque et al., 2017), wood anatomy (von Arx et al., 2016), and growth phenology (Cuny et al., 2015; Trouet et al., 2012). This is fortunate because these emerging fields are considerably advancing our

understanding of tree functioning, which will allow non-linearities and feedbacks to be mechanistically modeled and reconstructed (see Section 4). Yet, their sampling strategies are also not necessarily geared towards representing larger spatial scales with tree-ring observations. This diverse sampling background complicates upscaling of tree-ring information across all three steps:

(A) **Representing the whole tree**: Mature trees are usually sampled along the lower part of the stem, which is oldest and most accessible. How representative stem growth at this location is for the entire tree body depends on the dynamics of resource allocation and biomass formation. Assessing this variability would at a minimum require sampling individual trees at multiple heights, a laborious technique that is more readily applied to shrubs (Buchwal et al., 2013) but rarely performed on tall trees (but see e.g. Chhin et al., 2010; Monserud and Marshall, 2001; van der Maaten-Theunissen and Bouriaud, 2012). In addition, tree boles are never perfect cones and uncertainty due to collecting only few samples around the stem needs to be reduced (Bakker, 2005). Another limitation of most existing tree-ring records is that tree dimensions (e.g. diameter and height) at the time of sampling have not been recorded. This hampers the estimation and reconstruction of whole-tree volume or biomass – and thus the representation of absolute growth (Babst et al., 2014b). Aside from physical sampling, our limited understanding of tree-internal processes can bias ecophysiological conclusions drawn from tree-ring data. For instance, tree-ring stable isotope ratios differ from those of freshly produced carbohydrates in leaves because additional isotopic fractionation and mixing occur during transport and transitory storage (Gessler et al., 2014). These effects are not well understood.

(B) **Representing the site**: A traditional focus of tree-ring sampling has been on old and dominant individuals of a single species (Cook et al., 1995) that respond to a strong common environmental driver. This approach has served to maximize the common growth variability among trees, which could then be used, e.g. as a proxy for instrumentally measured climate variables or to reconstruct disturbance events. Such selective sampling clearly hampers the objective of quantifying forest growth, because failure to represent the full tree population at a site and over time can severely bias tree-ring estimates of biomass accumulation (Brienen et al., 2017; Nehrbass-Ahles et al., 2014; Peters et al., 2015). In addition, the documentation of most tree-ring records in public archives (e.g. the International Tree Ring Data Bank; ITRDB) is insufficient in terms of site extent, species composition, and forest age or size structure.

(C) **Representing larger spatial scales**: To represent tree growth across regions or even continents, ideal networks of tree-ring sites densely cover the geographic extent of the study area and reflect, in proportion to the area they occupy, the range of bioclimatic and ecological conditions experienced by species within this area. This ideal has probably rarely been achieved. Instead, traditional sampling for dendroclimatological purposes has often targeted areas with marginal growth conditions, which only occupy a small fraction of the landscape. We note, however, the difficulty of evaluating the spatial representativeness of existing networks because appropriate reference datasets are often lacking (see Section 2.1). If very large amounts of tree-ring data are compiled in mixed-species networks, their coverage can be more readily assessed. For example, a recent evaluation of the ITRDB indicated good coverage of climates with a mean annual temperature below 15 °C, whereas the spatial distribution of sites was strongly biased towards North America and Europe (Babst et al., 2017). Yet, even across these well-replicated continents, most records are subject to the above-mentioned sampling biases and the lack of biometric measurements restricts analyses to relative (i.e. detrended) growth variability and its climate response (Babst et al., 2013; Charney et al., 2016; St George and Ault, 2014). Going forward, it will be important to develop new tree-ring networks in more consistent and spatially representative ways (see Sections 2 and 3).

Uncertainties arising from the above-listed challenges may be more or less relevant in the context of a given study, but they generally propagate through all spatial scales (Fig. 1). This does not preclude tree rings from being used in global research, but emphasizes the need to i) understand how data are derived and ii) carefully treat data with explicit characterization of uncertainties. Hereafter, we review possibilities to facilitate the scaling of existing and newly collected tree-ring data with emphasis on quantifying tree growth and its drivers across increasingly large geographic and bioclimatic domains. In Section 2, we discuss statistical approaches to derive spatial patterns from existing networks, such as the ITRDB. Section 3 highlights possibilities to produce spatially explicit records of forest growth, by integrating the temporal information from tree rings with the spatial information from forest inventories and remotely sensed earth observations. Section 4 describes tree-ring and vegetation models of increasing complexity and scope that can provide a mechanistic understanding of tree growth, which is particularly relevant for predictions into future time frames. In addition to this general review, we provide in each section a practical and illustrative example related to tree ring-based inference at large scales. We end our article with some perspectives for future research.

2. Spatial patterns from detrended tree-ring data

2.1. On the climate sensitivity bias in global archives

Assessing the relationships between tree growth and monthly to seasonal climate has been a core objective of many tree-ring network analyses. This is because climate is the most important driver of inter-annual growth variability around the globe (St George and Ault, 2014) and long-term instrumental records of temperature, precipitation, and derivatives thereof are readily available. The obtained statistical relationships between radial tree growth and climate variation are strongest in areas where one or few climate parameters are highly limiting for growth (Fritts, 1976), for example at the cold or dry edge of a species' distribution range. These marginal growth environments (where trees often also live long) are frequently targeted by dendroclimatologists to maximize the co-variation of the tree-ring proxy with the desired climate parameter for reconstruction (e.g. Wilson et al., 2016). Hence, it seems likely that – even though palaeoclimatology is only one facet of tree-ring research – marginal sites are overrepresented in global tree-ring archives. Depending on its severity, this bias may enhance the derived magnitudes and biogeographic patterns in the climate response of forests (Babst et al., 2013; Charney et al., 2016; St George and Ault, 2014; Zhang et al., 2018) and the networks cannot be considered to be fully representative of forest growth at large scales.

Quantifying this potential oversensitivity to climate in large tree-ring archives requires the development of new, representative reference networks (see Section 3.1). Initial research in this direction suggests considerable geographic variation in the magnitude

of the climate sensitivity bias. For example, Klesse et al. (2018) found that ITRDB tree ring-width records in the US Southwest were 40–60% more sensitive to climate variation than surrounding samples collected in forest inventory plots. When the two datasets were used to estimate growth trends in response to projected climate change through 2099 in this region, the ITRDB trees implied a 41% greater decline in growth compared to the representative forest inventory sample. By contrast, a Europe-wide comparison of tree-ring data from the ITRDB against a newly collected network of sample plots showed no significant difference in climate sensitivity (Klesse et al., 2018). Hence, a general statement on the magnitude of the climate sensitivity bias in the ITRDB cannot be made at this point. Further evaluation efforts – including collating existing data not available through public repositories and/or developing new networks of tree-ring records – will be crucial to quantifying existing biases and increasing the representativeness of tree-ring archives for global forest growth. Also, further work on defining and using consistent metrics for sensitivity may be required to elucidate the magnitude and characteristics of this bias.

2.2. Statistical projection of relative growth variability

The collection of dense tree-ring networks worldwide and in near real-time is impractical. Hence, the goal of upscaling from sites to landscapes (scaling step C, Fig. 1) has to be achieved via the statistical projection (or mechanistic modeling, see Section 4) of tree growth across areas where measurements are missing. This is possible using empirically calibrated relationships between tree growth and its abiotic drivers. One limitation of this approach, however, is the small number of available predictor variables that are spatially resolved and cover sufficiently long time scales. Indeed, most remotely sensed earth observation records (e.g. of soil moisture, land cover, or forest disturbance regimes) are still not long enough to allow for the calibration of robust statistical models that could be used to predict tree growth. This leaves long-term gridded climate products (e.g. Harris et al., 2014) as the only option, with associated caveats when used in the context of bioclimatic niches (Ols et al., 2017). Predicting growth variability from climate alone is clearly a simplification of the highly complex set of drivers and responses that shape forests. Accordingly, higher-end calibration statistics for temperature reconstruction have achieved around 50–60% of the variance explained for the instrumental target (Wilson et al., 2016), whereas seasonal climate-growth relationships that emerge from large networks are on average much weaker (St George and Ault, 2014). In addition, the seasonality in climate response changes considerably between species and across climate space (Babst et al., 2013; Cook et al., 2001; Teets et al., 2018), making it impossible to globally attribute growth variability to climate during a single season. For all these reasons, novel and creative statistical approaches are needed to project radial growth variability at large spatial scales.

2.2.1. Practical example 1: towards gridded tree-ring width anomalies for Europe

Here we present and evaluate a machine learning approach to produce gridded tree-ring products at continental scales. We thereby pursue a purely statistical approach (as opposed to mechanistic formulations of biophysical processes; see Section 4) and estimate relative radial growth variability from a set of climatic predictor variables in a regression model. We used random decision forests (RDF; Breiman, 2001), a well-established technique that provides a flexible framework for learning nonparametric and nonlinear relationships when faced with many and collinear predictors. Our RDF models each contained 100 random decision trees and the final tree-ring width anomalies were predicted by averaging the outputs of each individual decision tree to prevent overfitting. RDF models need to be trained with observed datasets (Fig. 2). For this we used European tree-ring width chronologies from the ITRDB, detrended with a 30-year cubic smoothing spline, and climate data from the corresponding CRU TS-3.22 grid cells (Harris et al., 2014). Climate variables included monthly minimum, mean and maximum temperature, diurnal temperature range, ground frost frequency, precipitation, wet day frequency, vapor pressure, potential evapotranspiration, and cloud cover. Climate data from the preceding and current years (24 months in total) were entered in the model to account for lag effects frequently observed in tree-ring data (Zhang et al., 2018). The ITRDB contains enough data (~1000 European sites) to train individual RDF models separately for the most frequent tree genera (Table 2), many of which are primarily represented by one species. In addition, we trained a model where sites from all genera were pooled together. To evaluate model performance, we applied a leave-one-site-out cross-validation, under the condition that a specific chronology was only estimated based on other sites of the same genus that do not fall within the same CRU TS-3.22 grid cell (i.e. to prevent biases).

Across the entire European network, approximately 29% of the variance was explained (i.e. a Nash-Sutcliffe modeling efficiency (MEF; Nash and Sutcliffe, 1970) of about 0.29; Table 2). Importantly, RDF models with monthly predictors yielded stronger predictive accuracy compared to those with seasonally aggregated predictors. This emphasizes the relevance of changing seasonality in climate response across the represented climatic domains (Babst et al., 2013). The RDF models for individual genera performed similarly to the overall model (31–33% explained variance), except for *Larix* and *Pinus* where MEF was lower. For *Larix*, this is likely due to well-documented periodic defoliation by the Larch budmoth (Esper et al., 2007), which negatively affects growth and partly decouples it from its climatic drivers. Excluding known budmoth years is thus a possibility to improve future RDF predictions. For *Pinus*, the lower RDF performance could simply be related to the large number of *Pinus* species that are represented on the ITRDB, which increases both the distribution range and the diversity in climate response.

After the training phase described above, the inferred RDF models were combined with the gridded data products of the CRU TS-3.22 dataset to project radial growth anomalies across Europe, yielding annual raster maps of relative growth variability for each tree genus (Figure S1, Appendix A). Projection excluded those areas falling outside the geographic distribution of a given genus (referencing the 1 km^2 resolution distribution maps in the European Atlas of Forest Tree Species; de Rigo et al., 2016). Accordingly, a CRU TS-3.22 grid cell (0.5° resolution) was included, if it covered at least one smaller grid cell from the distribution maps that reported a presence of the genus at >5%. Encouragingly, our first results show clear differences in spatial growth variability among genera (Appendix A), even for those that belong to the same plant functional type. In addition to attributing these patterns to specific drivers, we are working on improving the RDF performance. This can potentially be achieved by including not only the inter-annual climate variability in the models, but also the long-term mean climatic conditions at each site. This way, the contrasting effects of, for instance, a warm anomaly under cold-humid (expected growth increase) *vs.* hot-dry (expected growth decrease) conditions can be better accounted for. Investigations at the species-level, rather than the genus-level, could also be explored in the future for potential improvements in modeling skill. In addition, we aim to consider non-climatic drivers in the RDF models as suitable spatial data become available.

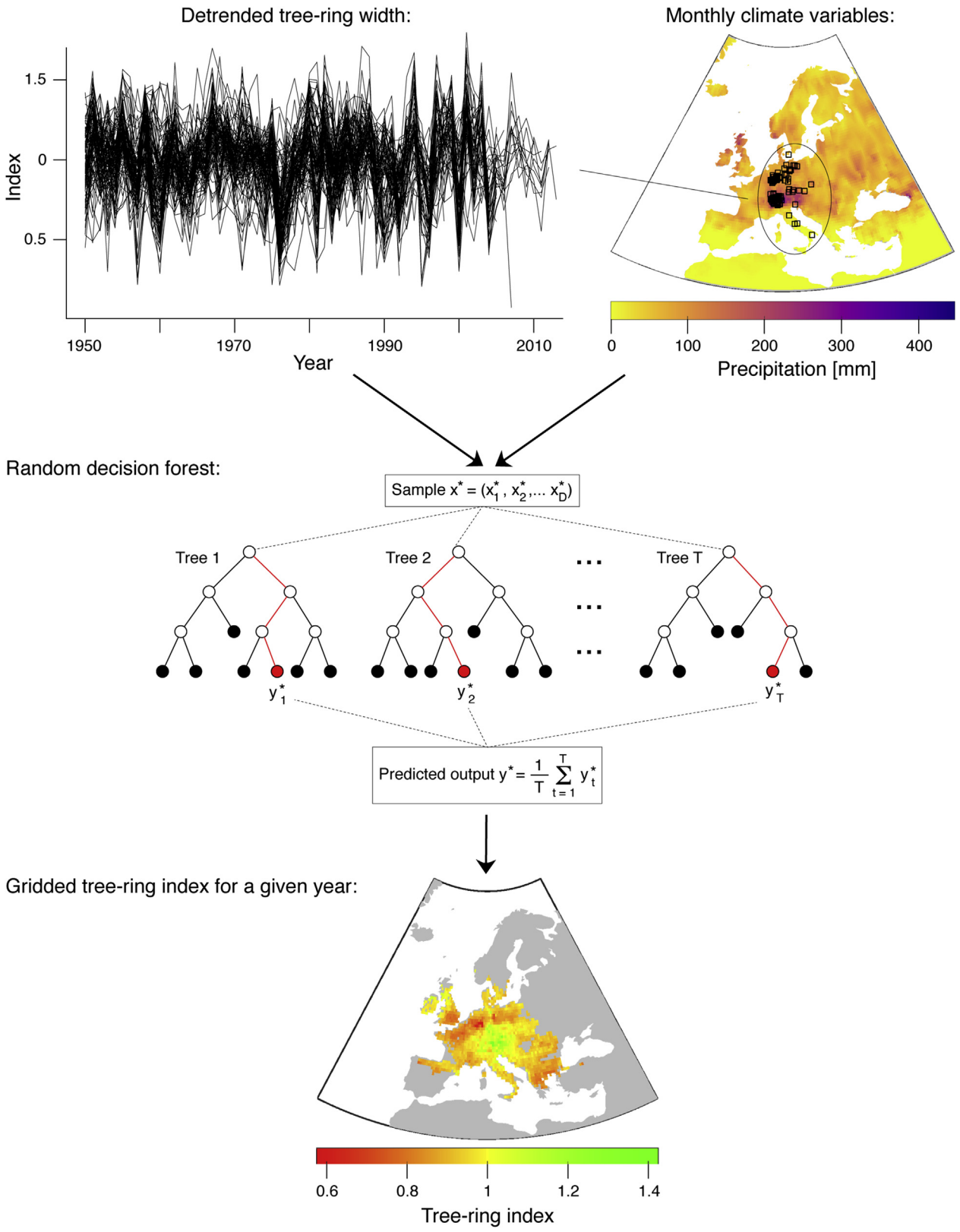

Fig. 2. Random decision forest approach to produce gridded projections of radial tree growth variability. This example includes all *Fagus sylvatica* sites that were available from the International Tree-Ring Data Bank as of October 2016.

Table 2
Performance of random forest regression models for predicting the growth variability of individual tree genera across Europe, assessed with a leave-one-site-out validation. Seasonal climatic predictors were aggregated for both the previous and current years (March–May; June–August; September–November) and the winter in between (December–February). MEF – Nash-Sutcliffe modeling efficiency; RMSE – root mean square error.

	Monthly predictor variables		Seasonal predictor variables	
Genus	MEF	RMSE	MEF	RMSE
Abies	0.329	0.146	0.261	0.527
Fagus	0.313	0.179	0.257	0.512
Larix	0.158	0.204	0.090	0.302
Picea	0.310	0.127	0.245	0.515
Pinus	0.240	0.130	0.173	0.430
Quercus	0.326	0.136	0.267	0.534
All sites	0.287	0.145	0.225	0.485

2.3. Spatially varying climate responses of radial tree growth

The statistical exercise presented in Section 2.2.1 assumes that the derived climate-growth relationships apply throughout the study domain, either across all species or in taxonomic groups (genera) – an assumption that we address in the following. It also showed that predicting relative growth variability from climate variability alone leaves a considerable fraction of the variance unexplained. By contrast, changes in the underlying climate-growth relationships should be more straightforward to predict and project because they follow gross biogeographic patterns (Babst et al., 2013; Charney et al., 2016). Indeed, a substantial body of literature has successfully mapped historical climate-growth relationships across space and time (Martin-Benito and Pederson, 2015; Restaino et al., 2016; St George and Ault, 2014). However, if the goal is to interpolate local observations of climate response across the intervening geographic space between unevenly distributed sites, a series of spatial challenges emerges. A first challenge relates to differences in the climate response among species at a given location (Teets et al., 2018). Accounting for such differences requires high-resolution maps of species composition for the entire target region, which may not exist everywhere and/or lack *in-situ* quality assessment (Serra-Diaz et al., 2017). Hence, the influence of species composition on the climate response of forests remains difficult to assess at large scales (Grossiord et al., 2014). A second challenge stems from limited information on micro-climate, nutrient availability, hydrology and topography. Such abiotic micro-site conditions can alter the climate response of trees (Nicklen et al., 2016; Salzer et al., 2009), but high-resolution data across the scaling area are rarely available. These two challenges are compounded by a third challenge: a shortage of tree-ring data for many species and certain ecoregions, especially in the tropics, that are severely under-represented in public archives (Babst et al., 2017).

These spatial challenges require finding a balance between the level of detail that is considered in an analysis, and the spatial scale that can be reached with the available data. One relatively simple option is to construct a single statistical model that describes growth as a function of the climatic niche that encompasses all trees within the scaling region, regardless of species (e.g. the "all sites" RDF model in Section 2.2.1). If we looked at a slice of this growth-climate function along one climate axis of the niche, we would expect it to look unimodal (Fig. 3a). However, the underlying function is multivariate, nonlinear, and relatively data-intensive to parameterize. In addition, this approach ignores species-specific drivers of tree growth (including pests and pathogens, Esper et al., 2007) and assumes that spatial differences in climate response can be solely attributed to gradients in the baseline climate, rather than to differences in species composition, competition, or other co-variates. In other words, site- and species-specific characteristics are averaged out for the sake of generalization, which may be necessary to reach very large spatial domains. In a global context, it may be plausible to subject all species to the same treatment because biogeographic patterns in climate response are generally more pronounced than differences between species (Fritts, 1976).

A refined version of this approach, while still pooling all species, is to construct separate growth-climate functions for geographic sub-areas ("response zones") of the target domain (Charney et al., 2016). This allows approximating the global response curve with a series of local linear models specific to these response zones (Fig. 3b). The zones themselves could be based on existing ecoregions (Omernik and Griffith, 2014) or other (e.g. geological) criteria to account for some of the missing non-climatic co-variates. Alternatively, they can be inferred from the climate responses contained in the tree-ring time series themselves. For instance, Charney et al. (2016) defined response zones by first clustering tree-ring sites across North America based on their climate correlation functions and then used an RDF analysis to assign all grid cells on the landscape to one of the clusters according to their baseline climates. This has the significant advantage that, as baseline climates shift in the future, both geographic (i.e. poleward) shifts in the response zones and changes in the climate sensitivity itself can be accounted for. Moving forward, a further refinement could be to capture variation in the local slopes of climate-growth relationships using models that include both long-term baseline climates and short-term climate anomalies (and interactions between them) as predictors of growth. In particular, this would capture continuous variation in climate-growth responses across climatic gradients.

Clearly the most precise approach is to construct the growth-climate function including the effects of individual species. Besides considering species-specific characteristics, this would also account for the fact that populations near the distribution limit are genetically adapted to respond less strongly to variability in limiting climatic drivers (Housset et al., 2018). However, detailed maps of species locations and composition would still be required to represent the actual climate response at a given location (de Rigo et al., 2016; Serra-Diaz et al., 2017) and weight the species-specific

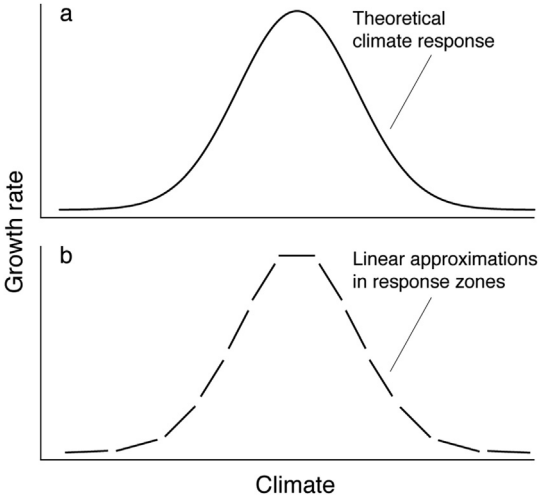

Fig. 3. Idealized growth rate as a function of a single climate variable across the target niche (a). This function can be approximated by a series of linear segments obtained from local climate response zones (b).

responses in a mixed species system. In addition, representative tree-ring data from across the entire target space are needed, which are currently not available for most species. Establishing this observational basis through data mining initiatives and especially the development of new and spatially representative tree-ring networks will be key to enabling the projection of species-specific climate responses with precision.

In contrast to the spatial challenges described above, temporal limitations to empirically forecasting the climate response will not be resolved by extensive and representative sampling. One reason for this is that the overlap between tree-ring and instrumental data is often limited to a few decades and extrapolation to future time frames is thus based on relatively short-term observations. This is problematic because the climate response is not only determined by how tree growth responds to climate on an inter-annual basis, but can be modified by longer-term climate patterns (Madrigal-González et al., 2017; Mendivelso et al., 2014) that are not captured in short time series. In addition, there may be a compounding effect when "ecological memory" leads to lagged responses after disturbances or climate anomalies (Ogle et al., 2015), or when a recurring climate anomaly alters the growth response itself (Brzostek et al., 2014; Galiano et al., 2012). For example, one hot summer may lead to only a minor decrease in growth rate in a drought-prone region, whereas a sequence of hot summers can cause increasingly dramatic growth declines. By contrast, there can be acclimation, wherein the recurrence of a climate anomaly (e.g. drought) lessens the strength of the growth response (Ainsworth and Long, 2005; Farrior et al., 2015). This is possible because trees are plastic organisms that can shift their resources over time, e.g. by growing more roots, restructuring branches, thickening the bark, or decreasing leaf size. Such physiological changes allow trees to better conserve water and return to normal growth more rapidly after a drought episode. Moreover, ecosystem-level responses to climate change will also influence the growth of trees. For example, drought induced mortality (Adams et al., 2017) often results in a reduction in stand density and living biomass. This process is similar to selective thinning that enhances growth and survival by sharing of available resources amongst fewer individuals (Clark et al., 2016). In addition, when we aim to forecast over time periods of generations, we have to consider the possibility of genetic adaptation and species migration (Aitken et al., 2008; Housset et al., 2018). Both of these processes tend to make future generations of trees growing at a location better suited to the new climate than the preceding generations. Finally, the trees of the future are likely to experience different combinations of temperature, precipitation, and atmospheric CO_2 concentrations than those in the past (Ainsworth and Long, 2005; Frank et al., 2015). Hence, any attempt to statistically forecast based on stationary observations from the past is always associated with increased uncertainty (Gustafson, 2013). For all of these reasons, an advanced mechanistic understanding of tree growth and climate response is needed (see Section 4).

3. Integration of tree rings with other ecological or earth observations

Tree-ring data offer decadal- to multi-centennial-length records of radial tree growth at annual to sub-annual resolution, allowing growth variability and its drivers to be investigated through time. However, quantifying absolute tree- and site-level growth (scaling steps A and B, Fig. 1) from tree rings requires additional information about tree architecture (i.e. allometries) and forest stand characteristics. This information is increasingly available from forest inventories and remotely sensed earth observations. In turn, tree-ring data can help compensate for the coarse temporal resolution of forest inventories (plots are typically revisited once every 3–10 years) and the generally short time-series of both data streams. Bringing together the temporal and spatial strengths of these three types of observations provides new opportunities to quantify tree growth across a range of scales (Zuidema and Frank, 2015).

3.1. Forest inventories

Tree rings have been used to assess tree growth in a forestry context since the mid-19th century, but it is only recently that collections made by forest inventory programs or in other permanent sample plots are being developed into data networks. Examples of these initiatives include Canada (Duchesne et al., 2017), the western United States (DeRose et al., 2017), Romania (Bouriaud et al., 2016), Mexico (G. Gutierez-Garcia, pers. comm.), and parts of the tropics (Brienen et al., 2016). These data have been used, for instance, to detect signals of CO_2 fertilization (Girardin et al., 2016) or to assess shifts in growth response to climate (Charru et al., 2017; D'Orangeville et al., 2016). Here we describe opportunities to quantify trends and temporal variability of tree growth that emerge from this type of tree-ring network. We also discuss statistical tools for integrating tree-ring with forest inventory data and thereby move beyond the traditional statistical modeling based solely on the principle limiting factors (Fritts, 1976). Finally, we identify some of the challenges that remain for combining tree-ring and forest inventory data into long-term records.

Collecting tree-ring data in a forest plot context can have three major advantages with respect to the scaling and projection of growth or aboveground biomass increment (ABI): 1) sampling can be performed in a comparatively representative or unbiased manner, 2) absolute rather than relative tree growth can be quantified, and 3) the inventory offers complementary information on the characteristics of the forest stand in which a tree is growing. Together, these advantages help overcome some of the limitations for estimating biomass growth associated with traditional tree-ring sampling (see Section 1.2). National forest inventory (NFI) programs are specifically designed to make estimates of forest characteristics (area or volume of forest; number and dimensions of trees) at large spatial scales from carefully designed networks of sampling plots (Bechtold and Patterson, 2005). The design may vary from one political entity to another (McRoberts et al., 2009), but their spatial representation of forested areas is essentially unparalleled. Within plots, the collection of increment cores in an objective manner with respect to tree species and size or age classes attempts to make sampling more representative of a forest (and overall forest growth) compared to that designed for dendroclimatological purposes (Nehrbass-Ahles et al., 2014). Tree-ring data collected in forest plots that are not part of an NFI (e.g. (Davis et al., 2009; Klesse et al., 2016) also make useful contributions to the overarching goal of building representative networks, particularly when the plots are arranged along environmental gradients (e.g., Buechling et al., 2017; Foster et al., 2016; Rollinson et al., 2016; Sánchez-Salguero et al., 2015). Ensuring "representativeness" within forest stands and across landscapes is key to addressing the heterogeneities, nonlinearities, and feedbacks that make scaling a challenge (Scholes, 2017).

Increment cores collected in forest plots are usually associated with measurements of tree dimensions and stand conditions. A measurement of diameter at breast height (DBH) at the time of sampling makes it possible to reconstruct annual tree diameter (Bakker, 2005), which can then be transformed into absolute estimates of tree growth (Alexander et al., 2017; Babst et al., 2014b). Analyzing absolute growth is key to addressing questions about the role of forests in the terrestrial carbon cycle and integrating tree-ring data with observed or simulated forest productivity (Babst

et al., 2014a; Klesse et al., 2018). In this context, metrics like basal area increment (BAI) and ABI are more useful and interpretable than relative growth variability generated by detrending raw tree-level measurements (Cook et al., 1995) to construct a site-level chronology. Besides the associated loss of inter-tree variability in absolute growth rates, detrending is one of the most subjective and debated aspects of tree-ring research because the choice of method critically affects the environmental information that is preserved in ring-width time-series (Cook, 1987; Melvin and Briffa, 2008; Sullivan and Csank, 2016).

Individual tree growth is also influenced by competition from neighboring trees, and in a carbon accounting context it becomes critical to quantify, understand, and project such demography-driven changes in forest growth (Chen et al., 2016; Trotsiuk et al., 2016). Capturing the influence of competition on individual tree growth is also key to scaling step B (Fig. 4) because individual tree growth both influences and is influenced by forest stand basal area, forming a self-regulating (density-dependent) feedback. Tree-ring data collected in a forest plot context allow for modeling the influence of forest stand conditions explicitly, as exemplified in several recent studies (Buechling et al., 2017; Foster et al., 2016; Rollinson et al., 2016; Sánchez-Salguero et al., 2015). Accounting for such *in-situ* information in statistical models is expected to produce more realistic predictions of tree growth compared to those based exclusively on climate variability.

These three characteristics of tree-ring data collected in a forest plot context – representativeness, absolute growth, and accompanying information on the forest stand and sampling design therein – enable the scaling from individual observations of bole diameter and radial increments to stand- and landscape-scale biomass accumulation (Fig. 4). Annual reconstructions of DBH can be transformed to whole tree biomass increments using allometric equations (scaling step A; Forrester et al., 2017). We note that the use of allometric equations is associated with its own set of uncertainties (Alexander et al., 2017; Nickless et al., 2011), some of which can be constrained with additional information derived from tree rings. For example, time series of wood density variation, combined with allometric estimates of tree volume, can improve estimates of whole-tree biomass increment (Bouriaud et al., 2015; Clough et al., 2017). Tree-level biomass increment can then be summed across individuals in the plot and adjusted by a known expansion factor (step B). Subsequently, the plot-level biomass estimates can be scaled to the target population using plot-level expansion factors or pre-determined sample-based estimators (Bechtold and Patterson, 2005). Alternatively, plot-level estimates are projected onto some other spatial scale using remote sensing observations (step C; Section 3.2; Jucker et al., 2017).

Integration of tree-ring and other forest inventory data can also take the form of data assimilation. The two data streams can, for example, be assimilated using a state-space model (Clark et al., 2007), or a hierarchical Bayesian model with two respective regressions linked by a constant of proportionality (Evans et al., 2017). Both of these statistical approaches can additionally take advantage of bole diameter re-measurement data for mixed datasets composed of trees with and without increment cores, and model the multiple influences on the growth of all individual trees explicitly. Assimilation of these two sources of information that describe the common process of tree growth advances our understanding of that process, while refining estimates of both process variability and measurement uncertainty. The ability to quantify both process variability and measurement uncertainty provides the opportunity to improve reconstructions and forecasts of forest growth and productivity at sites for which only one data type is available (Dietze et al., 2017). Finally, if forest inventory records are sufficiently long to inform about forest mortality, it becomes possible to characterize the relationship between growth and mortality. With a better understanding of the growth-mortality relationship, forest growth and productivity can be reconstructed further back in time.

An important limitation on long-term reconstructions of NFI plot-level growth arises from temporal changes in stand conditions (e.g., demography and competition). Specifically, trees alive at the time of sampling do not necessarily represent a random subset of the trees that once lived (i.e. the forest composition and characteristics back in time). While random or systematic sampling avoids the biases associated with the tree-selection principle of traditional dendroclimatology, other biases remain (e.g., slow-grower survivorship bias or fading record; Brienen et al., 2012; Swetnam et al., 1999). These pitfalls highlight the merits of establishing and maintaining permanent NFI remeasurement plots on a multi-decadal scale that can track temporal changes in stand conditions and complement time-series of climatic predictors in statistical models. However, most existing NFIs do not yet offer sufficient temporal depth to account for forest dynamics. One possible solution is to apply the best available empirical models of stand development (*i.e.*, growth-and-yield models, density management diagrams, empirical succession mapping) to reconstruct past stand conditions. Related (Bayesian) approaches may use state data assimilation or a state-space modeling framework to parameterize models of stand development from experimental forests where data do extend for several decades. Addressing the slow-grower survivorship bias and the competitive influence of trees that are no longer on the landscape will be crucial to fully realizing the research potential of paired tree-ring and forest plot data to

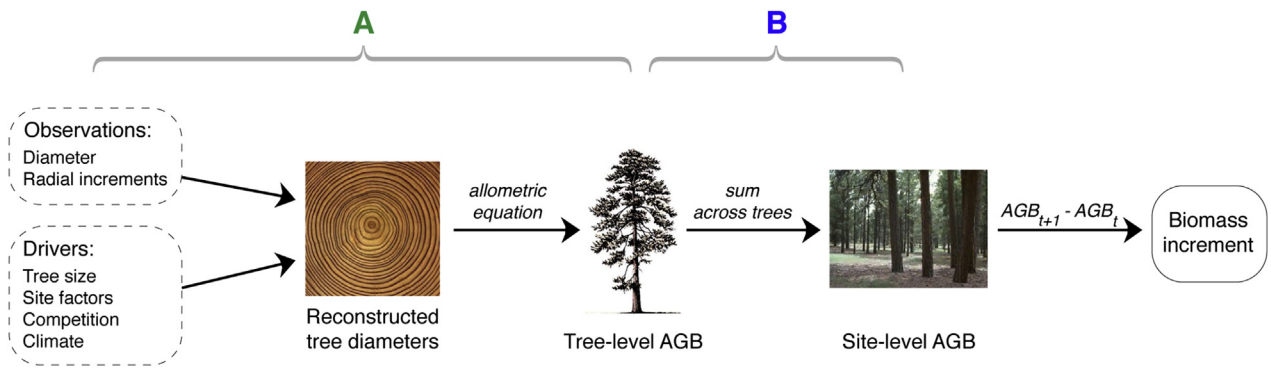

Fig. 4. Scaling of tree growth from observations of bole diameter and tree-ring width to tree- and site-level aboveground biomass (AGB) involves upscaling steps A and B. Forest plot data provide information on the drivers of tree growth, including site factors such as slope, aspect, soil conditions, stand-level basal area, and climate.

reconstruct forest growth in pre-inventory times.

3.2. Earth observations

Remotely sensed earth observations are a crucial tool for large-scale quantification and monitoring of ecosystem dynamics across space, and more recently also across time (e.g. Zhu et al., 2016). The increasing length of continuous satellite records, e.g. the Landsat Data Continuity Mission (LDCM), facilitates integration with temporally more coarsely resolved data such as tree rings (Vicente-Serrano et al., 2016). In addition, we emphasize here that the combination of tree-ring data with earth observations is not restricted to large-scale applications, but that it can support and advance all three scaling steps (Fig. 5). This is possible because – independent of the spatial scale – all information derived from remote sensing systems is fundamentally based on relating spectral reflectance data to field measurements via empirical models.

Terrestrial light detection and ranging data (LiDAR; also called terrestrial laser scanning, TLS) are the remotely sensed data most relevant at the individual tree scale. The application of TLS systems to characterize forest stands began about a decade ago (see Newnham et al., 2015 for a review) and recent methodological advances have included structural modeling of individual trees based on TLS point clouds (Åkerblom et al., 2015). The potential to estimate above-ground (and even below-ground; Liski et al., 2014) biomass from such data is increasingly explored (Calders et al., 2015). But similar to conventional forest inventory data (Section 3.1), TLS does not provide temporal information on tree growth. Hence, the integration of tree-ring and TLS data to reconstruct historical tree dimensions (scaling step A, Fig. 1) is promising, because it helps mitigate uncertainties related to the use of allometric functions and may offer a more precise representation of individual tree shapes (Wagner et al., 2017). Application of TLS in dense forest stands can, however, be complicated by occlusion effects (e.g. bushes or small trees blocking the view of the scanner), weather conditions (wind, precipitation, or fog), and limitations of the scanning device itself. The latter concern is mostly the coarser spatial resolution of distant tree parts (i.e. crowns) compared to that of lower stem parts, as well as the time it takes to scan an entire forest stand from a sufficient number of angles to produce a continuous point cloud. Both these methodological challenges and the expected benefits of integrating TLS data with tree-ring measurements to produce long-term tree volume reconstructions are yet to be explored.

Airborne remote sensing is showing the most potential for scaling to the site level (step B, Fig. 1). LiDAR can provide three-dimensional information about vegetation structure at local to regional scales and structure from motion photogrammetry (Westoby et al., 2012) can provide approximations thereof. Such information can be calibrated against *in-situ* data of basal area, canopy height, biomass, stand density, or leaf area to assess spatial variability in these parameters (Jucker et al., 2017). If repeated LiDAR flights are available, though still challenging, it is even possible to monitor temporal dynamics in integrated and height-specific canopy parameters (Griebel et al., 2017). Temporally resolved LiDAR data are still very rare, but should become more readily available with the increasing use of aircraft (Cunliffe et al., 2016) and drones (Tang and Shao, 2015) in forest monitoring programs. Because of the discontinuous data availability in both space and time, integration of airborne LiDAR with tree-ring records has so far been limited. This link will be strengthened in the future as advances are made on both sides: tree-ring sampling will become spatially more representative (Section 3.1); airborne LiDAR will increasingly be used to characterize not only larger forest stands, but also individual trees (Eysn et al., 2015), which can complement the application of TLS in complex stands. These efforts are converging towards more precise estimation and reconstruction of tree- and stand-level biomass and/or basal area increment.

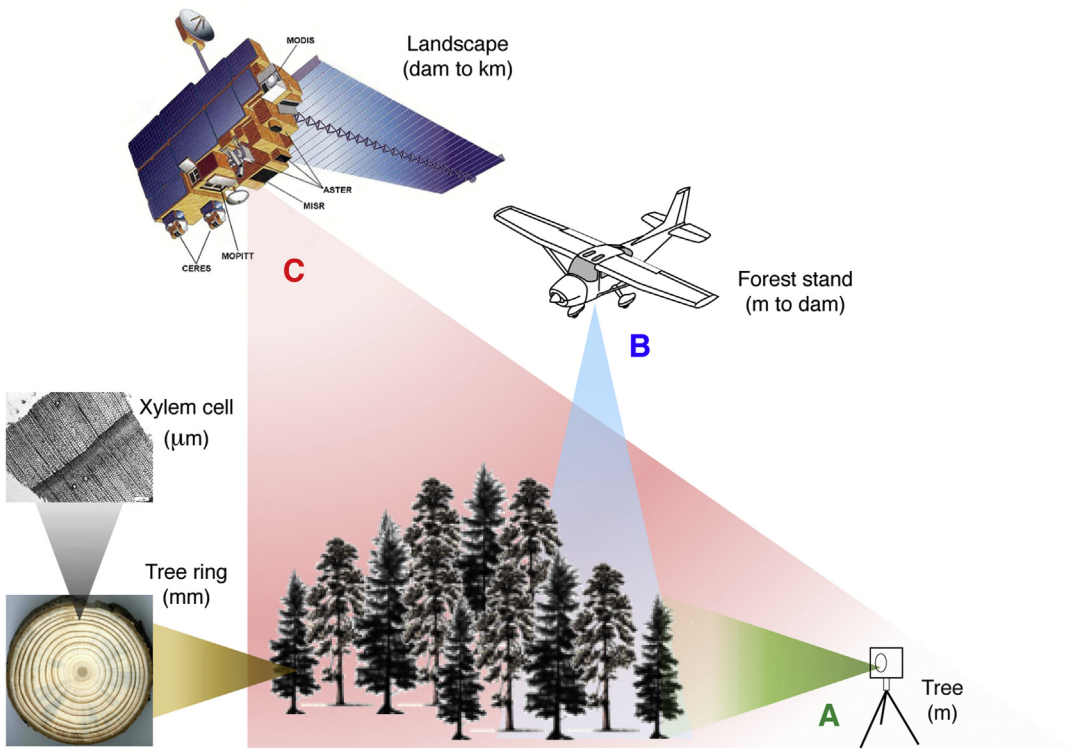

Fig. 5. Overview of the spatial scales at which tree-ring and remotely sensed observations can be integrated to support the three upscaling steps (A–C). dam - decameter.

While integration of tree-ring data with terrestrial and airborne LiDAR is still in its infancy, combining tree-ring and spectral data from polar-orbiting satellites is well established. Examples of environmental research that has used this combination include ecology (D'arrigo et al., 2000; Dorman et al., 2015; Huang et al., 2015), entomology (Çoban et al., 2014; Sangüesa-Barreda et al., 2014) and hydrology (Morales et al., 2015). For example, tree-ring data have been used to verify insect defoliation classifications inferred from remote sensing (Babst et al., 2010; Çoban et al., 2014), or as a proxy to reconstruct inter-annual fluctuations in lake area observed from Landsat time series (Morales et al., 2015). The satellite-derived parameter most frequently combined with tree rings has been the Normalized Difference Vegetation Index (NDVI), a measure of vegetation greenness. With now over thirty years of repeated observations, global data products such as the Global Inventory for Mapping and Modeling Studies (GIMMS; Tucker et al., 2005), have allowed for the comparison of tree-ring and NDVI responses to environmental change across a range of spatial and temporal scales (Coulthard et al., 2017; Kaufmann et al., 2004; Vicente-Serrano et al., 2013). The most common approaches have been to either compare the climate signals that are embedded in these two data streams (Del Castillo et al., 2015; Girardin et al., 2014; Pasho and Alla, 2015; Seftigen et al., in press), or to correlate time series of tree rings and NDVI directly (Beck et al., 2013; Berner et al., 2011; Bunn et al., 2013; D'arrigo et al., 2000; Girardin et al., 2016; Poulter et al., 2013; Vicente-Serrano et al., 2016). Generally, these studies have found a positive correlation of moderate strength between inter-annual NDVI variability and annual tree growth. However, there are notable exceptions along the North American Arctic treeline (Beck et al., 2013), in Europe (Pasho and Alla, 2015), and in parts of Canada (Girardin et al., 2016) where a significant positive correlation is not detected. These previous findings point to two main challenges associated with the integration of tree-ring and satellite observations.

The first challenge concerns the mismatch in spatial scale between site-level observations of tree rings and raster data from satellite sensors. The latter integrate surface reflectance information at various spatial scales, e.g., 30 m for Landsat, 250 m for MODIS, and 1–8 km for AVHRR. Each pixel integrates a mixture of species, disturbance histories, and land use activities that may affect the spectral information and complicate the comparison with single-species tree-ring chronologies. The second challenge emerges from temporal mismatches between the processes of canopy formation, leaf-level photosynthesis (observed by satellites), and wood formation (integrated in annual rings) in trees. The climate response of photosynthesis is more or less instantaneous, but there is a well-documented time lag between photosynthetic carbon uptake, growth, and biomass increment (Cuny et al., 2015). Furthermore, it is well known that climate variability can have lagged effects on tree growth via the storage and remobilization of carbohydrate reserves (Richardson et al., 2013; Fritts, 1976). For all these reasons, tree-ring data and vegetation indices cannot be expected to fully correspond, and the dynamics of these processes and associated temporal lags likely differ among ecosystems, species, and climatic domains.

3.2.1. Practical example 2: comparing tree-ring and NDVI data across Canada

To illustrate the temporal mismatch of canopy processes and stem growth, we compared tree-ring width, NDVI, and their correlations with monthly CRU TS-3.22 temperature (Harris et al., 2014) from the corresponding grid cells across Canada's boreal forest (Fig. 6). We obtained tree-ring width data from 598 plots (19 species) that were established as part of the Canadian NFI program. The tree-ring data were detrended using generalized negative exponential models and whitened (see Girardin et al., 2016 for details). For each plot, we obtained the corresponding GIMMS-3g NDVI record (Tucker et al., 2005), aggregated into a 0.5° regular grid using nearest-neighbor interpolation and subsequently averaged at monthly resolution. Point-wise Pearson correlations were computed among all three datasets over the 1982–2002 period. This analysis showed that tree-ring width and NDVI correlate in areas where they are both driven by temperature during the same season (Fig. 6). In some areas, however, the seasonality in the climate response differed clearly between NDVI and tree-ring width, which may at least partly explain why some studies report a spatially heterogeneous correlation between the two metrics (Beck et al., 2013; Girardin et al., 2016; Pasho and Alla, 2015). From this example it is evident that spatiotemporal patterns in tree-ring data and vegetation indices are not equivalent – their representation of different tree organs together with associated differences in processes and climatic drivers need to be considered in any comparison.

4. Mechanistic modeling of tree growth

Static statistical relationships derived from observations are clearly limited in terms of representing feedbacks in ecosystems (Scholes, 2017), and it is not clear how well these past relationships will serve to predict forest responses to the novel conditions in the Anthropocene. Hence, there is need to include more process information when linking wood formation to environmental variability, when reconstructing historical climate (Guiot et al., 2014), and especially when attempting to forecast into a future time frame (Gustafson, 2013). Fig. 7 illustrates the current range of tree-ring model complexity, from highly empirical monthly time-step approaches (e.g. Tolwinski-Ward et al., 2011) to highly physiological simulations of carbon and water flows in whole trees at very fine time steps (De Schepper and Steppe, 2010; Hölttä et al., 2010). A new approach is also shown within this scheme, with the objective of linking specific cambial-growth and whole-tree physiological models for global applications (see Section 4.2.1 for a description).

4.1. Simulating radial growth as a function of climatic controls

Wilson and Howard (1968) published the first model of intra-annual xylogenesis, which reproduced the daily cellular development throughout the growing season using “rules” to regulate cellular division, enlargement, wall thickening, and death. Realistic daily xylem development was simulated, but as no environmental controls were imposed (i.e. the rates of growth processes were model inputs), this approach can be considered “descriptive”. A handful of models were subsequently published (Howard and Wilson, 1972; Stevens, 1975; Wilson, 1973) that still required time-varying input parameters to produce realistic growth rings. To overcome these limitations, Fritts et al. (1991) developed a mechanistic model of daily cellular development called TRACH that was driven by temperature, water balance, and day length. This approach was already more general and relatively mechanistic, but it required as input the number of cells produced during the growing season and did not consider the supply of growth substrates (see Section 4.2). Expanding upon some of the ideas in TRACH, the now widely used Vaganov-Shashkin (VS) forward model of tree-ring formation (Vaganov et al., 2006) was developed. The VS model is built around the assumption that external multivariate environmental forcing exerts a direct and potentially nonlinear influence on secondary tree growth. Accordingly, tree rings and their internal structure (e.g. cell number and size) are simulated based on climatic controls on the kinetics of cell formation (Cuny et al., 2014; Rathgeber et al., 2016). The VS model includes

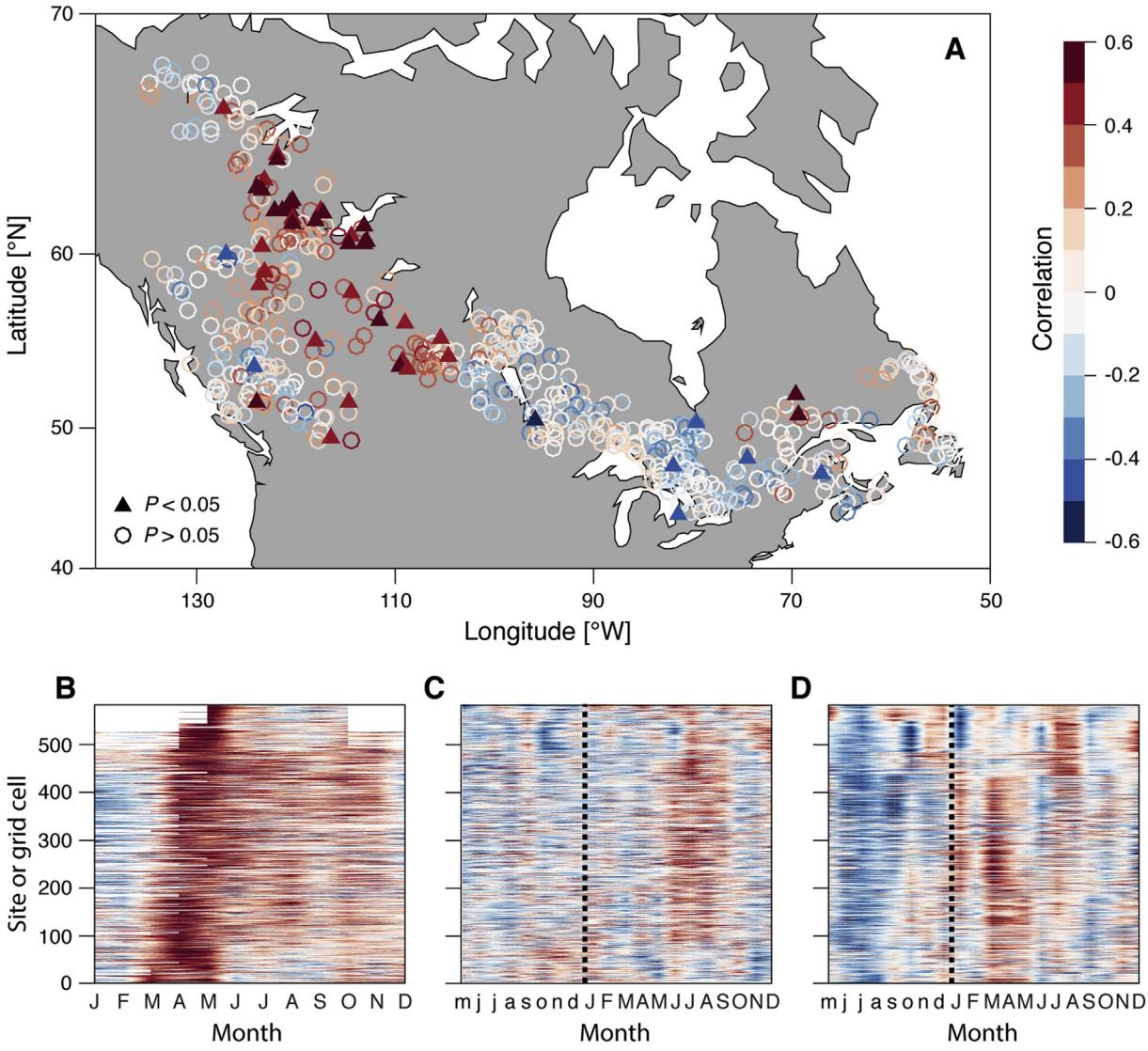

Fig. 6. Pearson correlation coefficients between detrended tree-ring width (TRW), the normalized difference vegetation index (NDVI), and temperature (tmp) over the 1982–2002 period. Panel (a): June–August NDVI *vs.* TRW; Panel (b): NDVI *vs.* tmp; Panel (c) June–August NDVI *vs.* tmp; Panel (d): TRW *vs.* tmp. Please note that sites and grid cells are ordered by increasing latitude in panels (b–d). Dashed lines separate the previous and current year.

two basic conditions for the non-linear dependence of wood formation on the environment: the Principle of Limiting Factor (Fritts, 1976) with respect to daily temperature and soil moisture, and a threshold growth response function to represent the dependence of cell formation on ambient temperature and soil moisture (Vaganov et al., 2006).

The output of the VS model includes synthetically generated standardized tree-ring indices that would be expected if local climate were the only external driver of tree growth. The skill of the VS model (unless fine-tuned for specific sites) is thereby roughly comparable to that achieved with statistical transfer function methods commonly applied in dendrochronology (Cook and Pederson, 2011; Evans et al., 2006). However, the VS model has significant advantages over purely statistical models in that it provides daily-resolved estimates of integral growth rates throughout the year and attributes them to different climatic drivers (Shishov et al., 2016). This greatly facilitates the interpretation of inter- and intra-annual growth patterns, for instance when capturing a reduction in radial growth rates during summer drought in Mediterranean areas (Touchan et al., 2012). The applicability of the VS model has also been demonstrated for other biomes across Asia and North America (Anchukaitis et al., 2006; Evans et al., 2006; Shi et al., 2008; Zhang et al., 2011). Comparisons between VS-simulated and observed tree-ring chronologies are particularly interesting, as they allow assessing whether temporal non-stationarity in climate-growth relationships arise from climate change alone (Anchukaitis et al., 2006), or from other abiotic or biotic sources.

Problematically, it is impractical to upscale site-level chronologies (step C, Fig. 1) using the VS model. This is because not all of the detailed information (more than 40 tunable input parameters) required to drive the simulation of cell-level processes is available at large spatial scales. Attempting to facilitate such large-scale application, a numerically more efficient forward tree-ring model, the Vaganov-Shaskin Lite (VSL), has been developed (Tolwinski-Ward et al., 2011). The VSL model excludes the cell-level processes and has thus been reduced to a product of three limiting climatic factors: temperature, soil water balance and solar radiation. Furthermore, it runs on monthly time steps and contains only 12 tunable parameters. Monthly-resolved climatic input data are

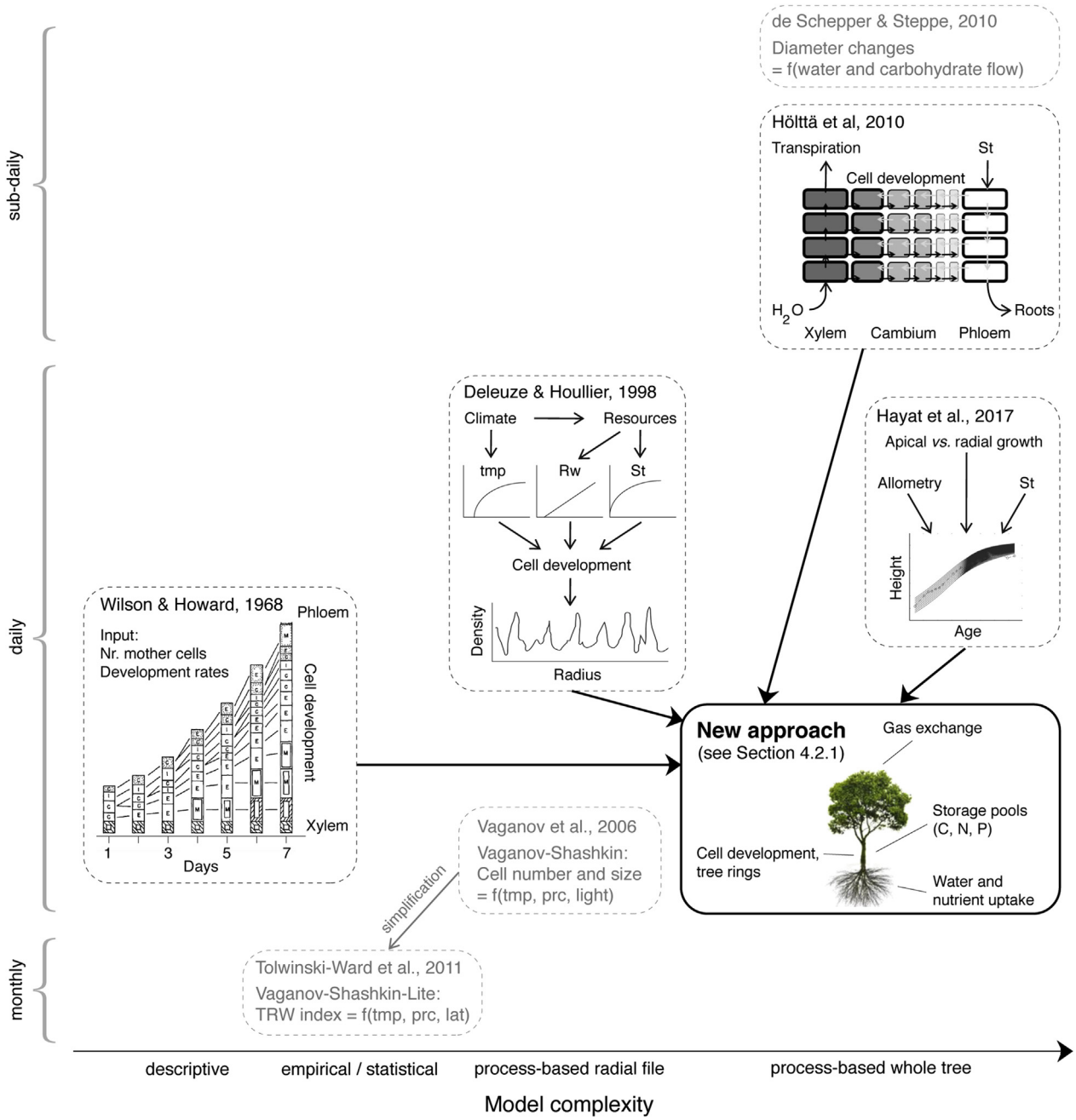

Fig. 7. Models of xylogenesis have been developed at different levels of complexity and across a range of temporal scales. Efforts are now being made to develop a new and broadly applicable modeling approach (Section 4.2.1) that will simulate whole tree growth as a function of environmental influences on physiological processes. Tmp – temperature; prc – precipitation; lat – latitude; St – photosynthates; Rw – soil moisture. The inset figures have been adapted from the cited publications, with permission from the respective publishers. The tree image is from infograph.venngage.com.

broadly available from meteorological stations and often contain much fewer gaps than daily observations. A disadvantage of this simplification is that the VSL model cannot resolve sub-monthly growth processes related to, for example, growth phenology and the formation of "false rings" (Touchan et al., 2012). In short, the VSL model is widely applicable and has been deemed capable of reproducing the variability in tree-ring width chronologies from more than 2000 sites on the ITRDB (Breitenmoser et al., 2014). Moreover, outputs from satellite Earth observations (Section 3.2) and dynamic global vegetation models (DGVMs; Section 4.3) are often provided at monthly resolution, making the VSL model a good candidate for pseudo-proxy experiments (Evans et al., 2013).

The VS and VSL models have proven valuable to study forest growth responses to climate variability and change, but they still only include climate variables as input parameters and do not consider other internal and external drivers of tree growth. The incorporation of the principle of limiting factors in these models is the primary constraint on their ability to forecast tree growth and its climate response beyond that of commonly employed statistical models (Section 2). An interesting prospect is to integrate these VS-type models with vegetation models that explicitly simulate relevant biological processes such as photosynthesis, respiration, and resource allocation. For example, Mina et al. (2016) demonstrated that simulations of stand basal area with the ForClim model

(Bugmann, 1996) could be improved by implementing the seasonal climate response of synthetic tree-ring chronologies from the VSL model. Such model-model integration approaches appear promising and should be extended to larger scales (e.g., using newly developing NFI networks; Section 3.1) and a variety of DGVMs.

4.2. Towards large-scale modeling of whole-tree growth

Tree rings are increasingly used to study the impacts of environmental change on forest ecosystems and carbon cycling (Babst et al., 2014a, 2017). For such applications, it is not sufficient to model only direct climate impacts on radial growth (Section 4.1). Models need to additionally account for indirect effects of changing external forcing (climate, CO_2, etc.) via canopy-level processes (Li et al., 2014). An early example of this is the model of Deleuze and Houllier (1998) that – similar to the VS model – was also designed to reduce the parameterization requirements of TRACH and predicts intra-annual wood density profiles of conifer species. In addition to simulating cambial cell division, enlargement, and wall thickening as functions of climate, their model assumes that wall thickening is co-limited by the supply of photosynthates, calculated from temperature and transpiration under the assumption of fixed foliar mass. This model has been successfully used to study intra-annual fluctuations in wood density, in combination with a more comprehensive treatment of plant water and photosynthate transport (Wilkinson et al., 2015). However, the implemented cohort approach to cellular differentiation limits comparisons with observed radial files (von Arx et al., 2016) and does not include scaling of radial-file growth to the whole tree.

Considering other processes and time-scales De Schepper and Steppe, 2010, developed a whole-tree model of reversible (diurnal fluctuations in water content) and irreversible (structural growth) stem diameter variations, using a very detailed representation of dynamic water and sugar transport between numerous levels in a tree on a time step of less than 1 s. Irreversible radial growth occurs as a function of local turgor and sugar content, but the focus of the model is on reversible changes. Hölttä et al., 2010 built on this model by adding cellular-level dynamics and thereby produced a remarkably comprehensive approach to modeling whole-tree growth, albeit omitting hormonal control. Their approach is very promising as a detailed physiological treatment and produces interesting conclusions regarding the effect of tree size on environmental influences. However, photosynthesis and transpiration are computed off-line, rather than as part of the model simulation, and a very large number of empirical parameters are required. Furthermore, the high-resolution time-stepping and consequent computing demands presently limit its application for large-scale studies of forest-environment interactions. Despite the knowledge of xylogenesis captured by these models, there is to date no generally applicable approach to modeling whole-tree growth at large scales. This would require a broadly applicable model structure with a few key parameter differences between plant functional types (or ideally species), as is currently implemented for photosynthesis in DGVMs (Section 4.3).

4.2.1. Practical example 3: towards a broadly applicable whole-tree model

Building on the approaches discussed above, a whole-tree model called “Grow_Up” is currently being constructed (Friend et al. in prep) that should be capable of being parameterized for any species and will be incorporated into a DGVM framework. A tree is assumed to grow as a coordinated whole, led by nutrient uptake and allocation, with foliage activity promoting cambial growth, resulting in demand for carbon and nutrients from the developing xylem. Cells in one lateral radial file per tree are represented, with the processes of division, enlargement, wall thickening, and death controlled by a range of external and internal factors (Fig. 8). The activities of apical meristems are also considered to enable whole-tree growth as described in (Hayat et al., 2017), an earlier version of this model. Reserve pools of carbon, nitrogen, and phosphorus enable carry-over effects between years, and the relative activities of the different meristems are controlled by shading, nutrient status, soil water, and phenological signals.

Three vectors are used to hold the state variables of the cells in the radial file: the cell development stage (i.e. cambial initial, xylem mother, enlarging, thickening, or mature), radial cell diameter, and cell wall thickness. When a cell matures, it is added to the tree stem and not treated further, although heartwood formation occurs in response to canopy die-back. The vectors start with the innermost immature cell along the radial file and end at the innermost phloem mother cell, which is a fixed anchor. The vectors are adjusted as cells are added through division or lost through maturation. The primary outputs directly derived from the xylogenetic component of Grow_Up are annual width and mass increment of the stem, as well as intra-ring density profiles. More detailed outputs such as the weekly kinetics of cellular development can also be produced for comparison with observations obtained using microcores (e.g. Cuny et al., 2014). This basic xylogenetic scheme is assumed to be universal in all tree species. However, the understanding of the rules governing cambial activation and dormancy, the rates of cellular division, transitions between cell types, rates of expansion, and rates of cell wall thickening, is currently incomplete and so the focus is now on testing various hypotheses.

Initial assumptions for the controls on the development of the radial file assume that the rates of growth of cambial, mother, and enlarging cells are influenced by water supply, temperature, a hormonal signal from the canopy, and the concentration of sugars in the cambium using simple response functions. Cambial cells divide when they reach a critical size, producing mother cells. Mother cells divide if they reach a critical size and transition to (non-dividing) enlarging cells when they reach a certain distance from the phloem. Enlarging cells enter the thickening phase once they reach a critical size, and thickening continues up to a critical limit at which the cell dies and becomes mature and functional xylem (see Fig. 8). The critical cell sizes and cell wall thicknesses, as well as the rates of thickening, are currently fixed parameters, with only the rates of cellular growth depending on environmental factors. These assumptions are being tested using microcores collected as components of various field campaigns and experiments (e.g. Cuny et al., 2014). This scheme is currently being implemented within the HYBRID9 DGVM framework (a derivative of the model of (Friend, 2010; Friend and White, 2000), and it is anticipated that this new approach will challenge the predictions of the current generation of DGVMs in fundamental ways, as well as open them up to direct comparison with tree-ring archives.

4.3. Tree-ring integration with ecophysiological and dynamic global vegetation models

Climate policy relies heavily on predictions from earth system models, including their crucial DGVM sub-components required to model terrestrial carbon fluxes, water exchange, and energy balances (Boucher et al., 2016). Current DGVMs struggle, however, to simulate forest growth and its climate response accurately, particularly at annual or longer time scales (Anderegg et al., 2015; Pappas et al., 2017; Rollinson et al., 2017; Tei et al., 2017). Hence, we see great potential for both tree-ring observations and ecophysiological models of tree growth to help evaluate and improve DGVMs. A conceptual challenge thereby is to reconcile the carbon source (i.e. photosynthesis) and sink limitations on tree growth (Fatichi

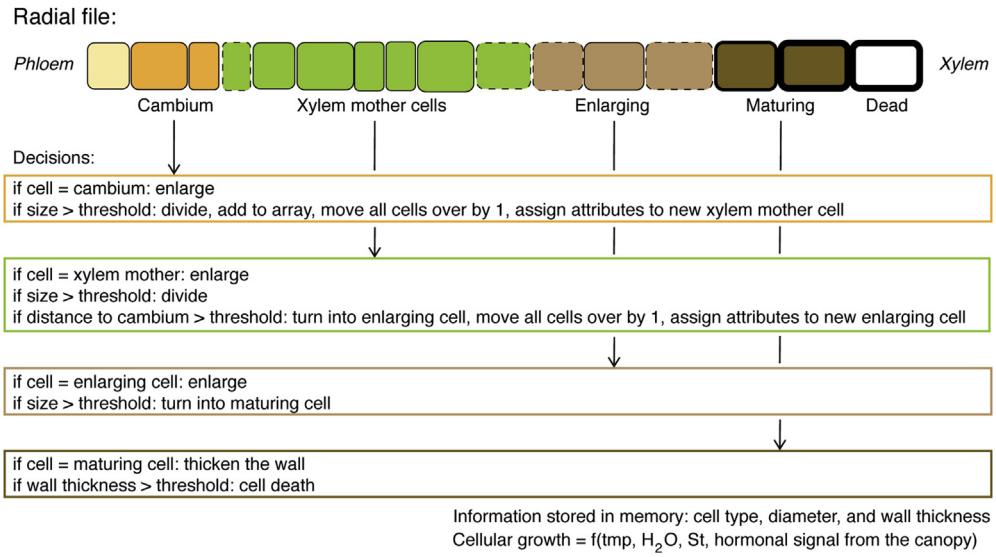
Radial file:
Phloem
Xylem
Cambium
Xylem mother cells
Enlarging
Maturing
Dead
Decisions:
if cell = cambium: enlarge
if size > threshold: divide, add to array, move all cells over by 1, assign attributes to new xylem mother cell
if cell = xylem mother: enlarge
if size > threshold: divide
if distance to cambium > threshold: turn into enlarging cell, move all cells over by 1, assign attributes to new enlarging cell
if cell = enlarging cell: enlarge
if size > threshold: turn into maturing cell
if cell = maturing cell: thicken the wall
if wall thickness > threshold: cell death
Information stored in memory: cell type, diameter, and wall thickness
Cellular growth = f(tmp, H2O, St, hormonal signal from the canopy)

Fig. 8. New model of cell development in a radial file using a vector approach and rules for cell differentiation based on internal and external drivers. Tmp – temperature; St - photosynthates.

et al., 2014; Körner, 2015). Sink limitations (see Section 4.1) and their possible feedbacks on photosynthesis are currently not implemented in DGVMs, which generates uncertainty (Friend et al., 2014) because growth is treated only as a downstream process. Explicitly representing xylogenesis in DGVMs (see Section 4.2.1), or at least evaluating DGVMs at stand and regional scales using ecophysiological models with explicit tree growth modules, could be a promising way to refine projections of terrestrial carbon cycling. Until this approach can be fully implemented and rigorously tested, tree rings should continue to be used in DGVM development by serving as observational references for model-data comparisons and model parameterization.

Past research has revealed a large spread in the ability of different DGVMs to reproduce patterns observed in tree rings. Besides being exceedingly sensitive to climate variability (Rollinson et al., 2017; Klesse et al., 2018), modeled NPP tends to recover much more quickly after extreme events (Anderegg et al., 2015) and lacks the memory effects that are commonly observed in tree-ring observations also in non-extreme years (Pappas et al., 2017). Accordingly, neither the significant correlations with previous year's climate, nor the positive auto-correlation structure of most tree-ring time series are simulated accurately. These findings point to deficits in the carbon allocation schemes that are implemented in current DGVMs (Sitch et al., 2015). Carbon allocation and turnover have been identified as an important source of uncertainty (Bloom et al., 2016; De Kauwe et al., 2014; Friend et al., 2014; Montané et al., 2017) that is compounded by a shortage of long-term observations of root and foliar dynamics.

The MAIDEN model (Misson, 2004), an ecophysiological model with a sophisticated carbon allocation scheme, has shown high correlations ($r > 0.5$) with tree-ring chronologies from coniferous and broadleaf species at Mediterranean and boreal sites (Gea-Izquierdo et al., 2015; Gennaretti et al., 2017). MAIDEN uses mechanistic rules for the temporal allocation of photosynthates to four carbon pools (leaves, stem, roots, and non-structural carbohydrates) according to phenological phases. While its large-scale application to estimate tree growth is still limited because certain allocation parameters need to be fitted site-by-site, the integration of the MAIDEN model with tree-ring observations has already been proposed with a view on paleo-applications. For instance (Guiot et al., 2014), have advocated the use of this and other ecophysiological models in the inverse mode to hindcast climate variability over centuries. In this application, the model parameters are first manually or automatically optimized to represent the observed radial increment. Using model-data-fusion techniques (Peng et al., 2011) the tree-ring data are then assimilated into the model to iteratively constrain the most likely climate conditions (i.e. probability distributions) that produce the observed radial increment in a given year (Boucher et al., 2014). For the pre-instrumental period when only tree-ring data are available, the climate probability distribution of a chosen reference (i.e. average) year is iteratively modified according to the annual tree-ring anomaly for that year (Guiot et al., 2014). This way, a climate probability distribution for each year of the reconstruction is determined. Such climate reconstructions based on ecophysiological models have the advantage over purely empirical calibrations that the influence of non-climatic effects that are represented in the model (e.g. CO_2) can be assessed. Additionally, mechanistic models are positioned to extract climatic information from tree-ring sites located away from the extreme growth environments typically considered for dendroclimatic reconstruction. Recalling that classical site selection practices for dendroclimatology were designed to optimize the signals from a single growth limiting factor (e.g., warm season temperatures or spring precipitation; see Section 2.1), vast areas where tree growth is influenced by multiple climatic parameters have remained more moderately utilized and primarily incorporated in drought reconstructions, whereby drought metrics such as the Palmer Drought Severity Index and the related tree-ring signals extracted are driven by both thermal and moisture conditions (e.g. Cook et al., 2015; Cook et al., 2004). Mechanistic models are positioned to identify separately the precipitation and temperature signals back in time embedded within tree-ring chronologies with mixed and temporally changing growth limitations.

With a view on DGVM development, model-data-fusion approaches involving tree-ring data (see above) could constrain carbon allocation to stem growth and thereby help evaluate and improve allocation schemes. In addition, a series of model intercomparison exercises would be useful to determine why some models perform better than others in simulating forest growth and its climate response. Such exercises are being conducted for various

ecosystem variables (see e.g. the MsTMIP project of the North American Carbon Program; https://nacp.ornl.gov/MsTMIP.shtml) and we are convinced that including tree-ring benchmarks from various ecoregions will be quite fruitful for providing quantitative insight in the representation of critical processes in DGVMs. However, one challenge for comparing multiple models with tree rings will be to generate parameters that are spatially and conceptually comparable. On one hand, estimates of absolute growth rates (e.g. in g C $m^{-2}y^{-1}$) from tree rings facilitate comparisons with standard DGVM output (e.g. net primary productivity, in g C $m^{-2}y^{-1}$). On the other hand, transforming radial growth into biomass increment generates uncertainty (see Section 3.1) that is best avoided if tree-ring data are to serve as an observational benchmark. Hence, we advocate that tree-ring width should become a standard output parameter (or "emergent property") of DGVMs and that the detail of the implemented carbon pools (leaves, branches, stem, coarse and fine roots, non-structural carbohydrates, etc.) in the models be re-examined for comparison with tree rings and other ecological data.

5. Perspectives for tree-ring research

Our discussion around the statistical scaling of tree-ring data in sections 2 and 3 has emphasized the need for representative sampling to capture the heterogeneity of forested landscapes. The systematic or random distribution of samples along the body of an individual tree, of individual trees within a site, and of sites across the landscape will allow for more robust past and future projections across the space where observations are sparse or missing. In addition, representative sampling of the area covered by the grid cells of raster data products should reduce the spatial mismatch between tree-ring data and satellite Earth observations or DGVM output. This objective of spatial representativeness is somewhat new to the field of dendrochronology. While other disciplines (e.g. ecosystem ecology or forestry) have a long history of optimizing sampling schemes for spatial or temporal scaling (Scholes, 2017), these ideas have only recently started to enter the broad scope of tree-ring research and require a certain rethinking of established protocols. For example, if tree-ring sampling should represent the absolute growth rates of a larger population of trees (e.g. a stand), the strength of the common growth variability among trees (traditionally assessed by the mean inter-series correlation) and metrics of how well a finite sample represents the theoretical population chronology (Expressed Population Signal; Buras, 2017; Cook and Peters, 1997; Wigley et al., 1984) are insufficient quality criteria. Hence, new quality criteria as well as guidelines for tree-ring sampling need to be established that serve both the needs of individual studies and the overarching goal of scaling. We recommend that this be done through interdisciplinary research initiatives that involve experts form complimentary disciplines, including dendrochronology, forest and landscape ecology, forestry, and statistical ecology.

At present, we have the best understanding of uncertainties in tree-ring data at the site level. Over the past years, a number of studies have characterized trend biases in time series of tree growth (e.g. Brienen et al., 2012; Brienen et al., 2017; Peters et al., 2015) or the impact of sampling practices on tree-ring quantification of stand-level above-ground biomass increment (Alexander et al., 2017; Nehrbass-Ahles et al., 2014). These studies will serve as important guidelines in future field campaigns. In contrast, sampling biases at the individual level are insufficiently constrained, especially when the goal is to represent full stem or tree-level growth. This is in part because the heterogeneity and dynamics of resource allocation to stem growth are not well understood. This could for example be tackled through intense sampling along trees that were commercially felled or uprooted after a storm. If combined with wood anatomical measurements (von Arx et al., 2016), such data could additionally serve as an improved test bed for mechanistic models of xylogenesis (Section 4). These models are becoming increasingly important tools to assess, reconstruct, and forecast tree growth responses to a changing environment because – even with the most representative sampling – statistical scaling is challenged by feedbacks in ecosystem processes (Scholes, 2017). Finally, uncertainties in tree-ring data will be the most challenging to assess at large spatial scales where individual- and site-level uncertainties cumulate and where the number of existing records may not suffice to counteract uncertainty from spatial heterogeneity. Yet, as new tree-ring and NFI data with well-quantified uncertainty are made accessible and interoperable across national boundaries, a global network of annually resolved forest biomass reconstructions can emerge. An important application of these data will then be to evaluate the ITRDB and ensure that this legacy of decades of tree-ring research can continue to support earth system science (Babst et al., 2017).

When tree rings go global – as is the theme of this review – the goal is to generate knowledge and data that can inform adaptation and mitigation strategies in the face of climate change. The primary strength of tree-ring records has so far been seen in their temporal depth that allows placing the current climatic variability and ongoing trends in a millennium-length context. Indeed, it is both important and disturbing to learn that the Earth is warming at an unprecedented rate (Esper et al., 2018; Wilson et al., 2016), that man-made influences on atmospheric circulation patterns can promote more frequent extreme events (e.g. through Arctic warming; Trouet et al., 2018), and that these events are directly linked to forest mortality, disturbances, and changes in the terrestrial carbon cycle (Schwalm et al., 2012, 2017; Williams et al., 2013). However, anthropogenic climate change is now considered indisputable and there is a need to transition towards tree-ring research that assesses, reconstructs and projects the responses and feedbacks of forest ecosystems to climate change. Dendrochronology can make important contributions at every step of successful scaling (Sections 2 and 3) and refined process understanding (Section 4). How and how quickly can we expect tree growth and its climate sensitivity to change with continued warming? Will thinning forests mitigate drought stress? How much carbon will be sequestered by forests under various management scenarios? By answering these and other relevant questions, tree-ring research can directly support the development and assessment of climate change adaptation strategies.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.07.009.

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